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THE EMBRYONIC DEVELOPMENT OF THE MARINE CADDIS FLY, *PHILANISUS PLEBEIUS* WALKER (TRICHOPTERA: CHATHAMIDAE)

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Among the few species of insects which spend all or part of their life cycle in marine habitats are certain caddis flies. These trichopterans comprise a single family, the Chathamidae. Adult chathamids inhabit coastal vegetation and their larvae live and develop in intertidal rock pools (Mosely and Kimmins, 1953; Riek, 1970, 1976). The family, which includes four species, is confined mainly to New Zealand and adjacent islands (Chatham Islands, Kermadec Islands), but one species, *Philanisus plebeius* Walker occurs both in New Zealand and along the coast of New South Wales (Riek, 1976). The larvae of *P. plebeius* are well known from rock pools in both localities. The adult female of *P. plebeius*, which has a strong pointed ovipositor, was thought to lay its eggs among coralline algae at periods of low tide (Riek, 1970, 1976). Anderson, Fletcher and Lawson-Kerr (1976), however, have recently shown that the ovipositor is used to insert the eggs into the coelom of one of the arms of a starfish. The host species for the eggs of *Philanisus plebeius* at Cape Banks, N.S.W., is the starfish *Patiriella exigua* Lamarck. The embryonic development of the caddis fly is completed within the starfish coelom, with escape to a free life as a first instar caddis larva. The present paper describes the embryonic development of *Philanisus plebeius* and the seasonal occurrence of oviposition in the host starfish population.

Materials and Methods

Thirty large specimens of *Patiriella exigua* were collected at monthly intervals from January to December, 1976, on the intertidal rock platform at Cape Banks, Botany Bay, N.S.W. In the laboratory, the starfish were opened by removal of the aboral body wall, and the coelomic cavities of the arms were inspected for the presence of *Philanisus* eggs (Fig. 1). The sex of the starfish was also noted. Batches of *Philanisus* eggs obtained in this manner were treated in two ways. After staging by direct observation of the state of development of the living embryos, the majority of egg masses were fixed in Kahle's fluid (formalin: alcohol: acetic acid, 6: 16: 1). Some batches of eggs were transferred to Petri dishes of sea water and maintained at 23–25° C, the water being changed every two days. In these culture conditions, the embryos continued to develop normally, allowing the timing of development and the external changes in the living embryo to be recorded.

Fixed embryos of different stages were dehydrated through methyl benzoate and benzene after piercing the chorion with a fine needle. The cleared embryos were then mounted unstained in Eukitt and used to elucidate further details of external structure at each stage.

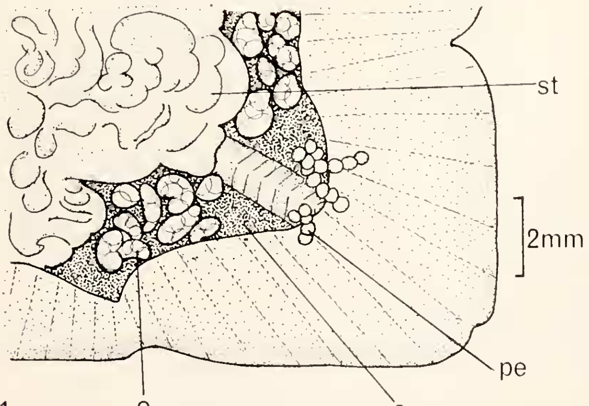
Results

Seasonal occurrence

Embryos of *Philanisus plebeius* were obtained from starfish hosts in every month of the year except the winter months of June and July, and the mid-summer month, January. The numbers of host starfish in each monthly sample of 30 individuals were as follows: January, 0; February, 6; March, 8; April, 2; May, 6; June, 0; July, 0; August, 2; September, 8; October, 8; November, 8; December, 1. In the majority of hosts, only one batch of eggs was found in each host individual. The eggs of a batch adhered loosely together and showed synchronous development, indicating that they had resulted from a single oviposition. The arm selected for oviposition was random, showing no fixed relationship with the madreporite and no discrimination of the sex of the host. In a few host individuals, two batches of eggs were found in different arms, one batch being advanced in development, the other early, clearly the result of separate ovipositions. None of the starfish examined were found to contain hatched, first instar larvae of *Philanisus,* although on several occasions hatching took place shortly after the host had been opened. The newly hatched larvae were very active and voracious, attacking the dissected host tissue. It seems likely that they eat their way out through the host body wall immediately after normal hatching.

Embryonic development

In each batch of eggs, 30–50 eggs are grouped together in short strings (Fig. 2), adhering loosely by chorionic contact. When transferred to sea water in a Petri dish, the individual eggs of a batch can be separated by light pressure with a fine dissecting needle.



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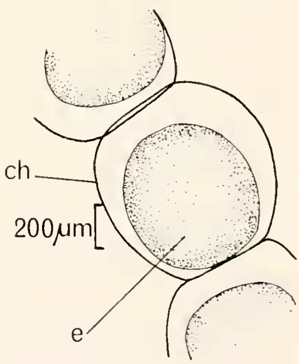

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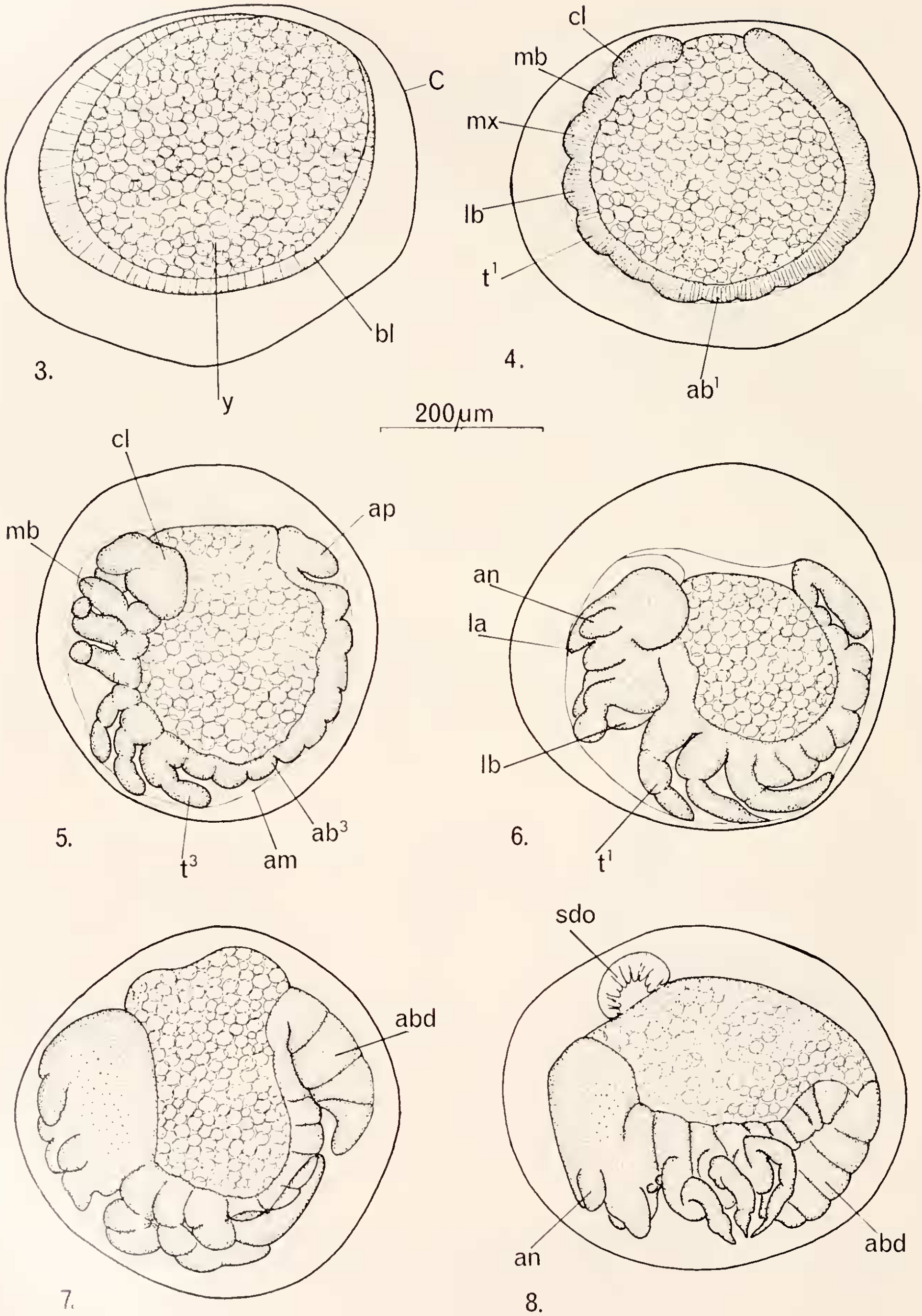
FIGURE 1. The eggs of the marine caddis fly, *Philanisus plebeius,* exposed by dissection of the oviposition host, the starfish *Patiriella exigua.* Abbreviations are: *c,* coelom; *o,* ovary; *pe,* egg of *Philanisus;* and *st,* stomach.

FIGURE 2. Part of an egg string of *Philanisus plebeius.* Abbreviations are: *ch,* chorion; and *e,* egg.



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In eggs observed shortly after oviposition, when the embryos are still at the stage of forming a germ band, each egg is ovoid, yellowish and densely yolky, with a long diameter of 0.27 mm. The transparent chorion which surrounds the egg is, in contrast, almost spherical and has a diameter of 0.39 mm. As development proceeds, the embryo enlarges to fill the space within the chorion. The chorionic diameter increases slightly before hatching takes place.

During the first three days of development, a blastoderm is formed at the yolk surface (Fig. 3), the embryonic primordium gradually differentiated, and an elongate, segmenting germ band is formed (Fig. 4). The segmenting germ band extends around most of the circumference of the egg along the ventral midline, with the end of the abdominal rudiment approaching the cephalic lobes. The mouthpart segments, thoracic segments and first few abdominal segments can be distinguished at this stage.

During the fourth to sixth days of development, the remaining abdominal segments become delineated, the cephalic lobes enlarge, antennal rudiments form and limb buds develop on the mouthpart and thoracic segments (Fig. 5). A pair of large rudiments of prolegs also forms on the tenth abdominal segment. On the seventh day, these limb buds increase further in length and begin to show podomere delineation. The mouthparts become more closely grouped together, while the thoracic limbs extend in a posterior direction beneath the ventral surface of the embryo, which retains its convex curvature (Fig. 6).

The embryo now performs a blastokinetic movement which reverses its curvature, from ventrally convex to ventrally concave, and is accompanied in its later phases by dorsal closure. This movement takes place through the eighth to ninth days. The first sign of blastokinesis is a downturning, tubulation, and forward thrust of the posterior end of the abdomen (Fig. 7). This movement proceeds until the entire abdomen is ventrally flexed (Figs. 8, 9), the yolk mass being now confined to the thorax and anterior part of the abdomen. At the same time, the bases of the thoracic limbs are shifted to a more lateral position on their respective segments. The stomodaeum and the elongating proctodaeum also become conspicuous during blastokinesis.

By the time the blastokinetic movement is complete (Fig. 10), the posterior end of the ventrally flexed abdomen is in contact with the head. Dorsal closure is complete, the remaining yolk is confined to the anterior part of the abdomen and secretion of the cuticle has begun. The remainder of the development of the embryo, from 10 days to hatching at 17–18 days is completed in this position

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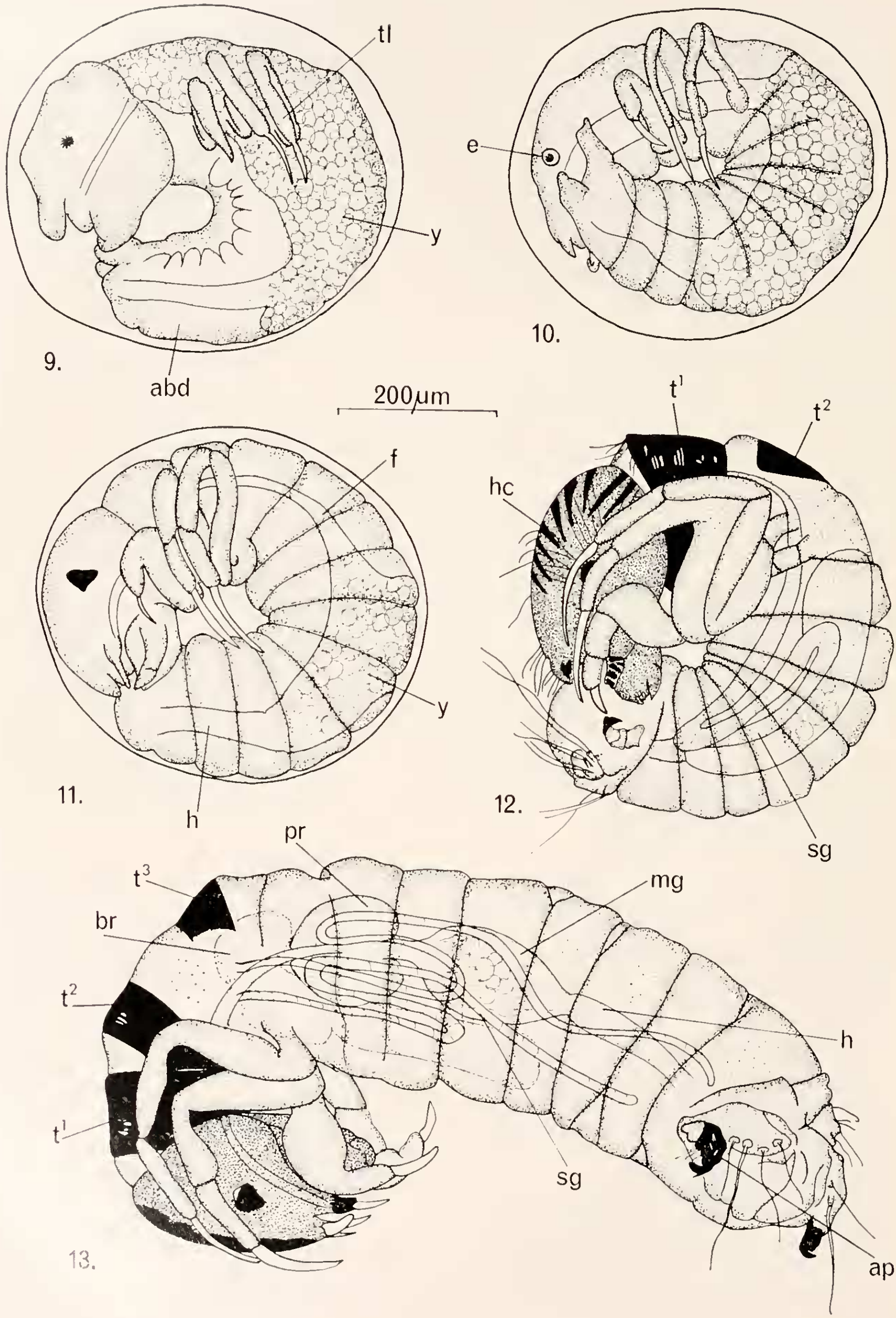
FIGURE 3. *Philanisus plebeius,* blastoderm stage. Abbreviations are: *bl,* blastoderm; *c,* chorion; and *y,* yolk.

FIGURE 4. *Philanisus plebeius,* segmenting germ band stage. Abbreviations are: ab^1, first abdominal segment; *cl,* cephalic lobe; *lb,* labium; *mb,* mandible; *mx,* maxilla; and t^1, first thoracic segment.

FIGURE 5. *Philanisus, plebeius,* early limb bud stage, 6 days. Abbreviations are: ab^3, third abdominal segment; *am,* amnion; *ap,* anal proleg; *cl,* cephalic lobe; *mb,* mandible; and t^3, third thoracic segment.

FIGURE 6. *Philanisus plebeius,* embryo approaching blastokinesis, 7 days. Abbreviations are: *an,* antenna; *la,* labrum; *lb,* labium; and t^1, first thoracic segment.

FIGURES 7 and 8. *Philanisus plebeius,* early stages in blastokinesis, 8 days. Abbreviations are: *abd,* abdomen; *an,* antenna; and *sdo,* serosal dorsal organ.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(Figs. 11, 12). The yolk reserves are gradually resorbed, only a small remnant persisting in the midgut when the larva hatches. Cuticularization of the head capsule, the first and second thoracic terga, the limbs and the abdominal prolegs becomes especially conspicuous during this period.

At hatching, the emerging larva (Fig. 13) is a typical trichopteran larva in both structure and movements. The mouthparts are functional, the larva crawls actively using the thoracic limbs, and a house is quickly constructed using available materials. If left among the tissues of the dissected host, the larva makes a house from pieces of broken starfish ossicle. Normally, the larva forms its house from pieces of material, mainly coralline alga, obtainable in its rock pool habitat.

Discussion

The present work confirms the fact, first pointed out by Anderson, Fletcher and Lawson-Kerr (1976), that *Philanisus plebeius* oviposits in the coelom of a host starfish, *Patiriella exigua,* and completes its embryonic development in the host coelom before hatching and escaping as a first instar larva.

In the *Philanisus* population of Cape Banks, N.S.W., oviposition occurs during most of the year, except for the winter months June and July and perhaps the midsummer month, January. Oviposition is active during the spring (September to November) and late summer to autumn (February to May). Since the duration of embryonic development is less than three weeks, young larvae might be expected to be present in the rock pools in the spring and autumn.

Riek (1976) provides data on the seasonal occurrence of larvae and pupae of *Philanisus plebeius* at Broulee, N.S.W., which support the concept of two breeding peaks at these times. He found that adults were present and young larvae were abundant during the spring, but that fully grown larvae and pupae predominated in December and Jaunary. Gravid adults then reappeared in February and persisted through the autumn.

It is not known at the present time whether the adults of *P. plebeius* have a short or an extended breeding life, nor how the species overwinters. The occurrence of oviposition in May suggests that a larval population is maintained during the winter months, emerging as adults in the following early spring. Overwintering by adults following emergence in late autumn is also a possibility.

Although the oviposition host of *P. plebeius* in New South Wales is *Patiriella exigua,* it seems likely that another host species of starfish is utilized in New Zealand, since *P. exigua* does not occur there (Anderson, Fletcher and Lawson-Kerr, 1976). The identity of this species remains to be established. The work

Figure 9. *Philanisus plebeius,* later stage in blastokinesis, 9 days. Abbreviations are: *abd,* abdomen; *tl,* thoracic limb; and *y,* yolk.

Figure 10. *Philanisus plebeius,* blastokinesis and dorsal closure complete, 10 days. Abbreviation is: *e,* eye.

Figure 11. *Philanisus plebeius,* embryo at 13 days. Abbreviations are: *f,* foregut; *h,* hindgut; and *y,* yolk.

Figure 12. *Philanisus plebeius,* embryo at 17 days, with chorion removed. Abbreviations are: *hc,* head capsule; *sg,* salivary gland; and t^1, t^2, thoracic segments.

Figure 13. *Philanisus plebeius,* newly hatched larva, 18 days after oviposition. Abbreviations are: *ap,* anal proleg; *br,* brain; *h,* hindgut; *mg,* midgut; *pr,* proventriculus; *sg,* salivary gland; and t^1, t^2, t^3, thoracic segments.

of Rick (1976) also shows that the females of the other three species of Chathamidae, *Philanisus fasciatus* in the Kermadec Islands, the brachypterous *Chathamia brevipennis* in the Chatham Islands and *Chathamia integripennis* in northern New Zealand, all have a strong pointed ovipositor similar to that of *P. plebeius*. It therefore seems likely that each species is associated with one or more species of starfish as an oviposition host. *C. brevipennis* has a rock pool larva similar to that of *P. plebeius*. The larvae of the other two species have not yet been described.

It is perhaps significant that the oviposition host of *P. plebeius, Patiriella exigua,* has an unusual breeding pattern, in which adults of both sexes maintain a constant state of reproductive maturity throughout the year, with spawning taking place opportunistically from time to time in response to appropriate environmental conditions (Lawson-Kerr and Anderson, unpublished). The coelomic cavity of the host species is thus not subject to the cyclic variation of gonad expansion and reduction that takes place in starfish species with an annual breeding cycle and a limited spawning season. The oviposition hosts of the other chathamid species may or may not show this phenomenon.

In spite of the unusual ovipostion site of *P. plebeius*, the eggs and mode of embryonic development of the species retain the typical trichopteran pattern. The only trichopteran species whose embryonic development has been studied in detail is *Stenopsyche griseipennis,* recently investigated by Miyakawa (1973, 1975). *S. griseipennis* oviposits on rock surfaces in freshwater streams. The egg is larger than that of *P. plebeius,* being 0.56 mm in length, but develops more rapidly, with hatching taking place after 12 days at 16–21° C. Miyakawa describes a remarkable invaginate formation of the embryonic primordium, but no comparison of this stage can be made for *P. plebeius,* due to a lack of critical early stages. Once the segmenting germ band has begun to elongate over the surface of the yolk mass, however, the development of the two species proceeds in a similar manner. The only notable difference associated with the smaller egg size in *P. plebeius,* 0.27 mm in length, is that the segmenting germ band extends further onto the dorsal surface of the yolk mass than in *S. griseipennis*. The middle period of development in both species is characterized by a blastokinesis, accompanied by dorsal closure, in which the curvature of the embryo is reversed within the egg space. This movement occupies three days in *S. griseipennis* and two days in *P. plebeius*. As Miyakawa (1975) points out, the trichopteran blastokinetic movement is a specialized embryonic movement shared with Lepidoptera (*e.g.,* Anderson, 1972; Wall, 1973), but differs from that of Lepidoptera in that the entire yolk mass of the trichopteran embryo is enclosed within the embryo in the usual pterygote manner. In Lepidoptera, much of the yolk mass is left outside the embryo during dorsal closure, to be consumed later through the mouth (Anderson and Wood, 1968).

The embryonic development of *P. plebeius,* therefore, shows no special structural modifications related to its intracoelomic site for development. The fact that the embryos continue to develop normally in sea water also excludes the possibility of any nutritional dependence. Possibly the major adaptive advantage of the oviposition relationship between *P. plebeius* and its starfish host lies in solving the problem of maintaining the eggs in the rock pool environment into which the larvae hatch. The eggs are loosely agglomerated and would, if laid among weed, be subject to wave dislodgement and to dessication during low tide. The starfish coelom provides a stable, protected environment for the embryos and eliminates the possibility of predation. As far as we are aware, no similar oviposition and embryonic development within the body cavity of an intertidal invertebrate host has been reported for any other species of insect. A major unsolved problem is how the newly hatched larvae escape from the host into the rock pool. Some modification of the normally carnivorous habit of a trichopteran larva is presumably involved.

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Summary

1. *P. plebeius,* a trichopteran with marine intertidal larvae, oviposits in the coelom of a starfish, *Patiriella exigua.* Oviposition occurs mainly in the spring and autumn months.

2. In spite of the intracoelomic location of the embryos, the development of *P. plebeius* follows an unmodified trichopteran mode, including the characteristic blastokinesis. Nutrients are not supplied to the caddis embryos by the host starfish.

3. Hatching takes place in the starfish coelom after 17–18 days. The newly hatched caddis larvae quickly escape to their rock pool habitat.

4. The form of the female ovipositor indicates that other species of Chathamidae utilize starfish species as oviposition hosts.

5. This mode of oviposition offers protection to the caddis embryos in the intertidal habitat.

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